ANA VEIGA

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ROLE IN THE PROJECT

Review and examine all published data of seasonality pattern and duration across four species of sea turtles, namely, loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), hawksbill (*Eretmochelys imbricata*) and green turtle (*Chelonia mydas*) at a global scale. Analyse the data and do the write-up.

PROBLEMS EXPERIENCED

Originally this project was designed to include all the seven species of sea turtles. However, due to lack of reliable published data from the restricted number of nesting sites under study for olive ridley (*Lepidochelys olivacea*), Kemp's ridley (*Lepidochelys kempi*) and flatback turtle (*Natator depressus*), these species were excluded from this study.
There were also important nesting sites that were not included in this study because seasonality of nesting data was not available or the available data did not cover the full nesting season.

TARGET JOURNAL

Marine Ecology Progress Series

REASONS FOR CHOICE OF THE TARGET JOURNAL

This happens to be one of the leading journals in the field of marine ecology. It maintains a high standard of quality for scientific contributions and contains relevant topical research studies. I have chosen this journal because I favour its writing style and I feel the topics it publishes are closest to my topic of research.

Seasonality and Temperature:

Turtles in Hot Water?

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ABSTRACT: Variation in temperature affects the biology of sea turtles at a range of scales. To elucidate the drivers of seasonality of nesting and duration of season, databases across four species of sea turtles (*Caretta caretta* n=37, *Chelonia mydas* n=64, *Dermochelys coriacea* n=44 and *Eretmochelys imbricata* n=36) at a global scale were created. By using remotely sensed sea surface temperature data, thermal profiles across the nesting season were generated. Duration of nesting season was correlated with latitude in all species but was more tightly coupled with temperature; seasons were significantly longer with increased mean SST. In general, nesting seasonality occurred at warmest time of the year. SST for the month before, month after and the month of peak nesting significantly affected the month of peak nesting.

KEY WORDS: Seasonality • Sea Surface Temperature • Latitude • *Caretta caretta* • *Chelonia mydas* • *Dermochelys coriacea* • *Eretmochelys imbricata* • Sea turtles

INTRODUCTION

As with all ectothermic animals, temperature has a profound influence on the life history of sea turtles (Davenport 1997). Variation in temperature affects the biology of this group at a range of scales. Sea turtles are globally distributed throughout the tropical and subtropical seas (Mazaris et al. 2008) and may experience and tolerate widely different temperatures (Mrosovsky 1980). For instance, leatherbacks (*Dermochelys coriacea*) swim far into the northern and southern hemispheres, loggerhead turtles (*Caretta caretta*) have a sub-tropical nesting range (Mrosovsky 1980), Kemp's ridley (*Lepidochelys kempi*) and other species are found in New England waters (Lazell, 1980). Adult sea turtles migrate hundreds to thousands of kilometres between specific feeding and breeding areas (Plotkin 2003). In addition, at the start of cold season, they migrate toward warmer waters and to avoid cold stunning, larger turtles may enter a hibernation-like state (Milton & Lutz 2003). It has also been reported that during the overwintering phase, there is an increase in the period spent on the seabed for green turtles and loggerheads as a result of long resting dives (Broderick et al. 2007). Moreover, hyperthermia is unusual when turtles are in the ocean but can be experienced while they are on land, basking or nesting (Milton & Lutz 2003). Thus, both high and low

temperatures have negative impacts on sea turtles physiology, affecting feeding behaviour, acid-base and ion balance, and stress hormone levels (Milton & Lutz 2003). Food availability and temperature influence sea turtles' growth rates (Heppell et al. 2003) which is decelerated by cold temperature (Mrosovsky 1980). Temperature also has a profound impact on their reproduction in several ways which I outline in turn.

Sea turtles show temperature-dependent sex determination (TSD) (Bull 1980), with cooler nests producing predominantly males and warm nests producing predominantly females (Morreale et al. 1982). Approximately equal numbers of males and females are produced at pivotal temperatures (Yntema & Mrosovky 1982). Furthermore, the sex ratio of offspring differs at different times of the year (Mrosovsky et al. 1984). The period when gender is determined by temperature occurs during the middle third of development of embryos (Standora & Spotila 1985). Temperature also influences the duration of incubation (Miller 1985), it is longer at cooler temperatures (Mrosovsky 1980).

In general, female sea turtles do not breed in consecutive years (Davenport 1997), but spend two or more years feeding at sea between successive nesting years (Solow et al. 2002). Males and females do not necessarily have to use the same time scale for reproduction (Miller 1997). The time for two successive seasons at the beach is defined as remigration interval (Carr & Carr 1972). Moreover, the mean remigration interval reported for females differs among the species (Miller 1997). Solow et al. (2002) reported that increased sea surface temperature (SST) has a positive effect on the 2-year remigration probability in the second winter following nesting for green turtles (*Chelonia mydas*) in Tortuguero, Costa Rica, with thermally dependent process affecting nutritional status in the previous winter sufficient to sustain vitellogenesis. For Pacific loggerhead population, Chaloupka et al. (2008) reported that there was a significant inverse correlation between nesting abundance and mean SST, because warmer foraging habitats are probably associated with decreased ocean productivity and prey abundance and therefore decreased breeding capacity.

Nesting season for most populations are constrained temporally (Hamman et al. 2003) and occurs predominantly during the warmer months (Miller 1997). But for some populations, it may occur year-round with seasonal peak and trough periods (Miller 1997). It is generally assumed that nesting season length is shorter at higher latitude beaches (Weishampel et al. 2004) and that nesting activity increases with ocean temperature and photoperiod (Williams-Walls et al. 1983). Nesting seasonality is probably a result of females adjusting their reproductive activity to coincide with conditions that contribute most to maximize reproductive fitness (Cheng 2009 et al.).

The impact of temperature on seasonality of nesting has not yet been thoroughly analysed across species at a global scale. Understanding these impacts will help to better predict the effects of climate change on these species. To address this issue, I reviewed and examined all published information on seasonality across four species of marine turtles: loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), hawksbill (*Eretmochelys imbricata*) and green turtle (*Chelonia mydas*). The other three species, namely, olive ridley (*Lepidochelys olivacea*), Kemp's ridley (*Lepidochelys kempi*) and flatback turtle (*Natator depressus*) were excluded from this study due to lack of reliable published data from the restricted number of nesting sites under study for these species. The specific question asked was: What are the key drivers of seasonality pattern and duration?

MATERIALS AND METHODS

Seasonality of nesting. A database of the monthly distribution of nests in a season from different regions for four species of marine turtles (*Caretta caretta*, *Chelonia mydas, Dermochelys coriacea* and *Eretmochelys imbricata*) was created. The nesting season data were obtained from published literature. Where data were only presented graphically, figures were digitized. Criteria for selecting the data were as follows: 1) data must have covered the full nesting season; 2) only data that provides the number of clutches laid daily, weekly or monthly were included. All data were aggregated by month. In cases where data were for more than one nesting season, the mean number of nests for each month was calculated.

Duration of season. An additional database was created for the duration of nesting season (in months). In this case, even data for sites for which only a date range was given could be included.

Locations. For locations of all study sites, see Fig. 1-3. Latitude in decimal degrees ca. 5km offshore for each region, were considered as the distance from the equator.

SST data. For every site and for the corresponding year-range, SST was obtained from Hadley Ice and Sea Surface Temperature (Hadley ISST) dataset for data prior to 1985 and from Advanced Very High Resolution Radiometer (AVHRR) dataset for data after 1985. For sites for which the year that the nesting season was defined was not given, the mean SST for the five years prior to the publication date was selected.

Statistical analyses. Data were analysed using GenStat (11^{th} Edition). Test for the assumptions for normal distribution were performed prior to all analyses, and in case assumptions were not met adequate transformations were made. Linear mixed effects models with restricted maximum likelihood (REML) analysis were constructed to determine the factor that dictates the duration of nesting season and the month of peak nesting. Differences were considered significant at $P<0.05$.

RESULTS

A total of 66 populations from 53 sites (*Caretta caretta* n=17; *Chelonia mydas* n=19; *Dermochelys coriacea* n=19; *Eretmochelys imbricata* n=11) and 115 populations from 97 sites (*C. caretta* n= 20; *C. mydas* n=45; *D. coriacea* n=25; *E. imbricata* n=25) were included for the seasonality of nesting and for the duration of season, respectively. It worth noting that some sites yielded data for more than one species.

Duration of nest season

The mean season duration in months was 4.4 ± 1.2 (range of 3-8 months) for *Caretta caretta*, 7.8 ± 3.4 (range of 3-12 months) for *Chelonia mydas*, 6.5 ± 2.8 (range of 3-12 months) for *Dermochelys coriacea* and 7.6 ± 3.1 (range of 3-12 months) for *Eretmochelys imbricata* (Fig. 4). Duration was broadly correlated with latitude in all four species (Fig. 5).

To fully elucidate the drivers of seasonal duration I sought to construct a model including species, latitude and mean SST. Due to a high correlation between distance from the equator and mean SST (r^2=0.62) the model was first run with both mean SST and distance degrees as fixed effects, however, SST was significant and distance degrees was not but alone both terms were significant. SST and species were incorporated as fixed effects in the linear mixed model, site was included as a random effect. Duration of nesting season was significantly longer with increased mean SST (Linear Mixed Effects Model, Wald statistic = 29.04, $p < 0.01$) but was not significantly affected by species (Linear Mixed Effects Model, Wald statistic = 5.91, $p = 0.13$).

Seasonality of nesting

In general, nesting seasonality occurred at warmest time of the year (Fig. 6). To elucidate how SST affects seasonality I constructed a model of how the proportion of nesting may have been driven by SST in peak month or each of the 2 months before and after. SST for the month before, month after and the month of peak nesting significantly affected the month of peak nesting (respectively: Linear Mixed Effects Model, Wald statistic = 5.32, $p < 0.05$; Wald statistic = 5.59, $p < 0.05$; and Wald statistic = 6.94, $p < 0.01$). However, the SST two months before and two months after the month of peak nesting did not influence the month of peak nesting.

DISCUSSION

Temperature and photoperiod will differ in strength and intensity especially along a latitudinal gradient (Hamann et al. 2003). Thus, it is generally assumed that duration of a nesting season (defined as the period of first and the last clutches laid during a year) is determined by latitude, being usually shorter on higher latitudes where summer is comparatively shorter than in the tropics. Although the results of this study showed this was the case, the length of a nesting season was dictated much more by SST: it was generally longer in hotter sites.

However, previous studies reported contrasting findings: Mazaris et al. (2008) found no significant difference between SST and duration of nesting season for the Mediterranean loggerhead population. Pike et al. (2006) found that nesting season was shorter with increasing SST for loggerhead population nesting along the Atlantic coast of central Florida (USA), and Hawkes et al. (2007) reported that the duration of the nesting season in warmer years was significantly longer for loggerheads nesting along Atlantic coast of North Carolina

(USA). Although SST is probably the main predictor of duration of a nesting season, it is possible that there are also other factors, apart from latitude, that determine the duration of a nesting season. This may explain these contrasting findings; however, more research is needed on the inter-relationships of factors affecting duration of a nesting season.

From my research findings, nesting season generally occurred in the warmest months for the four species of marine turtles but there were exceptions. For instance, in Masira Island, Oman (Fig. 2, site 64), the highest proportion of *Caretta caretta* nests occurred in the coolest month. Other exceptions occurred in Mafia Island, Tanzania, where higher proportions of *Chelonia mydas* nests also occurred in relatively colder months (Fig. 2, site 52; Fig. 6-h); and in Playon de Mexiquillo, Mexico, where during the warmest months no nesting occurred for *Dermochelys coriacea* (Fig. 1, site 16; Fig. 6-k).

To paraphrase Owens (1980), "eggs must be on the beach at the right time of year", because successful incubation is only possible within certain thermal limits (Davenport 1997). Indeed, Godley et al. (2002) reported that for the population of green turtles (*Chelonia mydas*) nesting at Ascension Island, little or no nesting occurs with sand temperatures being close to or below critical limits for development. Futhermore, at warmer temperatures a female is able to re-nest sooner (Hays et al. 2002) as the length of the internesting interval decreases when the water is warmer (Sato et al. 1998). Further research needs to be conducted to look at the possible linkage between the length of internesting interval and the peak nesting month.

Hawkes et al. (2007) suggested that fundamental and realised thermal niches for nesting may not essentially be the same. If this is true, for some populations the optimal time to nest may not be at the warmest month. This also helps to prevent extremely skewed sex ratios. It can be assumed that if the peak of nest season coincides with one of the warmest months of the year, more female offspring will probably be produced. Indeed, Freedberg and Wade (2001) hypothesize that female-biased sex ratios in reptiles with TSD are strengthened by natal nest site fidelity of females. Futhermore, global warming may result in a strong sex ratio bias that could lead to extinction (Hulin et al. 2009). Although shifts in behaviour related to environmental warming are occurring (Weishampel et al. 2004), it remains to be seen if sea turtles could change the timing of reproduction (Hulin et al. 2009).

There are definite advantages to the positive correlation between peak of nesting and warm temperatures. These include better conditions for egg incubation. However, as we have seen, this positive correlation does not always hold true and the reasons for this remain unanswered. Strong evidence has been presented that SST is the key driver of seasonality pattern and duration. Nesting seasons were longer with increased SST. Thus in the context of global warming, it is possible that rookeries that are experiencing an increase in SST may also see an increase in the length of nesting season and strong sex ratio bias. Unfortunately, the current study was limited by the availability of published data. I hope that more data on seasonality across all species of marine turtles will be published. Further research might then investigate the effects of SST on the duration of nest season and on the month of peak nesting for the populations and the species excluded from this analysis.

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FIGURE LEGENDS

Fig. 1. Nesting sites in the Americas. ***Caretta caretta***: 1=Topsail Island, USA (Beasley et al. 1998) 2=Cape Remain, U.S.A (Caldwell et al. 1959) 3=Georgia, USA (Scott 2006) 4=Canaveral National Seashore, Florida, USA (Pike & Stiner 2007) 5=Jupiter Island, USA (Engeman et al. 2006) 6= Broward County, Florida (Burney et al. 1990) 10=Cayman Islands (Aiken et al. 2002) 26= Buritaca, Colombia (Hirth 1980) 42=Espírito Santo State, Brazil (Baptistotte et al. 2003). ***Chelonia mydas***: 4=Canaveral National Seashore, Florida, U.S.A (Pike & Stiner 2007) 5= Jupiter Island, Florida, USA (Engeman et al. 2005) 8= El Cuyo, Yucatan, Mexico (Zambrano & Rodríguez 1995) 9= Cuba (Hirth 1997) 10= Cayman Islands (Bell et al. 2007) 11= Dominican Republic (Hirth 1997) 12=Puerto Rico (Hirth 1997) 15=Revillagigedo Archipelago, Mexico (Juarez-Ceron et al. 2003) 19=St. Kitts, West Indies (Butler 2001) 20=Belize (Hirth 1997) 21=Martinique (Hirth 1997) 23=El Salvador (Hirth 1997) 29=Tortuguero, Costa Rica (Tiwari et al. 2006) 35=Krofajapasi, Suriname (Mrosovsky et al. 1984b) 38=Colombia (Hirth 1997) 39=Atol das Rocas, Brazil (Hirth 1997) 41=Praia do Forte, Brazil (Hirth 1997). ***Dermochelys coriacea***: 4=Canaveral National Seashore, Florida, USA (Pike & Stiner 2007) 13= Humacao Beaches, Puerto Rico (Rivera-Muñiz et al. 2002) 14= British Virgin Islands (McGowan et al. 2008) 16= Playon de Mexiquillo, Mexico (Martinez et al. 2006) 18= Sandy Point, U.S. Virgin Islands (Eckert & Eckert 1984) 19= St. Kitts, West Indies (Butler 2001) 27= Trinidad Island (Hirth 1980) 28=Grande Riviere Beach, Trinidad and Tobago (Lum 2005) 30=Playa Langosta, Costa Rica (Chaves et al. 1996) 32=Gandoca Beach, Costa Rica (Chacón-Chaverri & Eckert 2007) 33=Chiriqui Beach, Panama (Ordoñez et al. 2007) 36=Baboensanti, Suriname (Hilterman 2001) 37=Ya:lima:po beach, French Guiana (Girondot et al. 2006) 43= State of Espírito Santo (north coast), Brazil (Thomé et al. 2007). ***Eretmochelys imbricata***: 7= The Bahamas (Witzell 1983) 8= El Cuyo, Yucatan, Mexico (Pérez-Castañeda et al. 2007) 13= Humacao Beaches, Puerto Rico (Chárriez-Serrano et al. 2002) 17= Buck Island Reef National Monument, U.S.A (Hillis 1990) 19= St. Kitts, West Indies (Butler 2001) 22= Saint Lucia (Witzell 1983) 24=Barbados (Beggs et al. 2007) 25=Pearl Cays, Nicaragua (Lagueux et al. 2003) 31=Venezuela (Witzell 1983) 34=Suriname (Witzell 1983) 38=Colombia (Witzell 1983) 40=Arembepe and Praia do Forte, Bahia, Brazil (Marcovaldi et al. 1999). Solid circles indicate sites for which data were available on seasonality and season duration. Open circles indicate sites for which only seasonal duration were available.

Fig. 2. Nesting sites in Africa and Middle East. ***Caretta caretta***: 44=Boavista island, Cape Verde (Lopez et al 2003) 54=Tongaland, South Africa (Hughes 1974) 55= Kuriat Islands, Tunisia (Jribi et al. 2006) 56= Laganas Bay, Zakynthos island, Greece (Margaritoulis, D. 2005) 57= Fethiye Beach, Turkey (Baran and Türkozan 1996) 58= Samandağ Beach, Turkey (Yalçin-Özdilek 2007) 60= Alagadi Beach, Cyprus (Broderick & Godley 2000) 64= Masira, Oman (Ross 1979). ***Chelonia mydas****:* 45=Poilão, Bijagós Archipelago, Guinea-Bissau (Catry et al. 2002) 46=Ivory Coast (Peñate et al. 2007) 47=South of Bioko Island, Equatorial Guinea (Tomás et al. 1999) 49=Republic of Congo (Bal et al. 2007) 50=Ascension Island (Mortimer & Carr 1987) 52=Mafia Island, Tanzania (Muir & Abdallah 2006) 53=Aldabra Atoll (Hirth 1997) 58=Samandağ Beach, Turkey (Yalçin-Özdilek 2007) 59=Latakia beach, Siria (Rees et

al. 2008) 60=Alagadi Beach, Cyprus (Broderick & Godley 2000) 63=Saih Al-Marai, Oman (Alkindi et al. 2006). ***Dermochelys coriacea***: 46=Ivory Coast (Peñate et al. 2007) 47=South of Bioko Island, Equatorial Guinea (Tomás et al. 1999) 48=Gamba, Gabon (Witt et al. in press) 49=Republic of Congo (Bal et al. 2007) 54=Tongaland, South Africa (Hughes 1974). ***Eretmochelys imbricata***: 47=South of Bioko Island, Equatorial Guinea (Tomás et al. 1999) 51=Cousin Island, Seychelles (Mortimer & Bresson 1999) 61= Karan, Kurayn, Jana and Jurayd islands, Arabian Gulf (Pilcher 1999) 65= Oman (Witzell 1983) 66=Jabal Aziz , South Yemen (Hirth 1980). Solid circles indicate sites for which data were available on seasonality and season duration. Open circles indicate sites for which only seasonal duration were available.

Fig. 3. Nesting sites in Asia and Oceania. ***Caretta caretta***: 70= Ryukyu Archipelago (Kamezaki 1986) 74= Senri Beach, Japan (Sato et al. 1997) 95= Mon Repos, Australia (Chu et al. 2008). ***Chelonia mydas***: 62=Hawkes Bay and Sandspit, Pakistan (Asrar 1999) 67=Gujarat coast, India (Sunderraj & Joshua 2006) 68= St. Martin Island, Bangladesh (Islam 2006) 69= Lanyu (Orchid Island), Taiwan (Cheng et al. 2009) 71= Xisha Islands, China (Hirth 1997) 75=Tern Island, Hawai (Niethammer et al. 1997) 77=Huyong Island, Thailand (Yasuda et al. 2006) 78=Sri Lanka, Kosgoda (Hirth 1997) 81=Sarawak, Malaysia (Hirth 1997) 82=Maldives(Hirth 1997) 86=Phoenix Islands (Hirth 1997) 87=Long Island, Papua New Guinea (Hirth 1997) 89=Berau Islands, Indonesia (Hirth 1997) 92= Gulf of Carpentaria, Australia (Limpus 2008) 93= Northern Great Barrier Reef, Australia (Limpus 2008) 94=South Queensland, Australia (Limpus 2008) 97=Fiji (Hirth 1997). ***Dermochelys coriacea***: 80=Rantau Abang, Malaysia (Chua 1988) 83=Jamursba-Medi, Papua, Indonesia (Hitipeuw et al. 2007) 84=Wermon, Papua, Indonesia (Hitipeuw et al. 2007) 88=Kamiali WMA, Papua New Guinea (Benson et al. 2007) 96=Southeastern Queensland, Australia (Limpus 2009). ***Eretmochelys imbricata***: 70= Ryukyu Archipelago (Kamezaki 1986) 72= Philippines (Witzell 1983) 73=Thailand (Witzell 1983) 76= Palau Is, Micronesia (Hirth 1980) 79=Pulau Gulisaan, Malaysia (Pilcher & Ali 1999) 85=Gresik, Indonesia (Suganuma et al. 1999) 90=Solomon Islands, Australia (Limpus 2009) 91=Torres Strait, Australia (Limpus 2009). Solid circles indicate sites for which data were available on seasonality and season duration. Open circles indicate sites for which only seasonal duration were available. For logistical purposes site 86 (Phoenix Islands) is not shown.

Fig. 4. Range of temperature for nesting (a) and for the month of peak nesting (b) for each species. *Caretta caretta* (Cc), *Chelonia mydas* (Cm), *Dermochelys coriacea* (Dc) and *Eretmochelys imbricata* (Ei).

Fig. 5. Relationships between latitude degrees from the equator and duration of nest season (transformed to normalize data) for each species. (a) *Caretta caretta* ($r^2 = 0.13$), (b) *Chelonia mydas* ($r^2 = 0.27$), (c) *Dermochelys coriacea* ($r^2 = 0.29$) and (d) *Eretmochelys imbricata* ($r^2 = 0.03$).

Fig. 6. Seasonal distribution of nests and variation of SST. *Caretta caretta*: a – Jupiter Island, Florida (U.S.A); b – Grand Cayman, Cayman Islands; c – Espírito Santo state, Brazil; d – Boavista Island, Cape Verde; e – Alagadi beach, Northern Cyprus. *Chelonia mydas*: f – Jupiter Island, Florida (U.S.A); g – Tortuguero, Costa Rica; h – Mafia Island, Tanzania; i-Huyong Island, Thailand; j-Tern Island, Hawai. *Dermochelys coriacea*: k – Playon de Mexiquillo, Mexico; l – St. Kitts, West Indies; m – Gandoca Beach, Costa Rica; n – Gamba, Gabon; o – South of Bioko Island, Equatorial Guinea. *Eretmochelys imbricata*: p – El Cuyo, Yucatan Peninsula, Mexico; q – Barbados; r – Pearl Cays, Nicaragua; s – Arembepe and Praia do Forte, Bahia, Brazil; t – Arabian Gulf (islands: Karan, Kurayn, Jana and Jurayd).

FIGURES

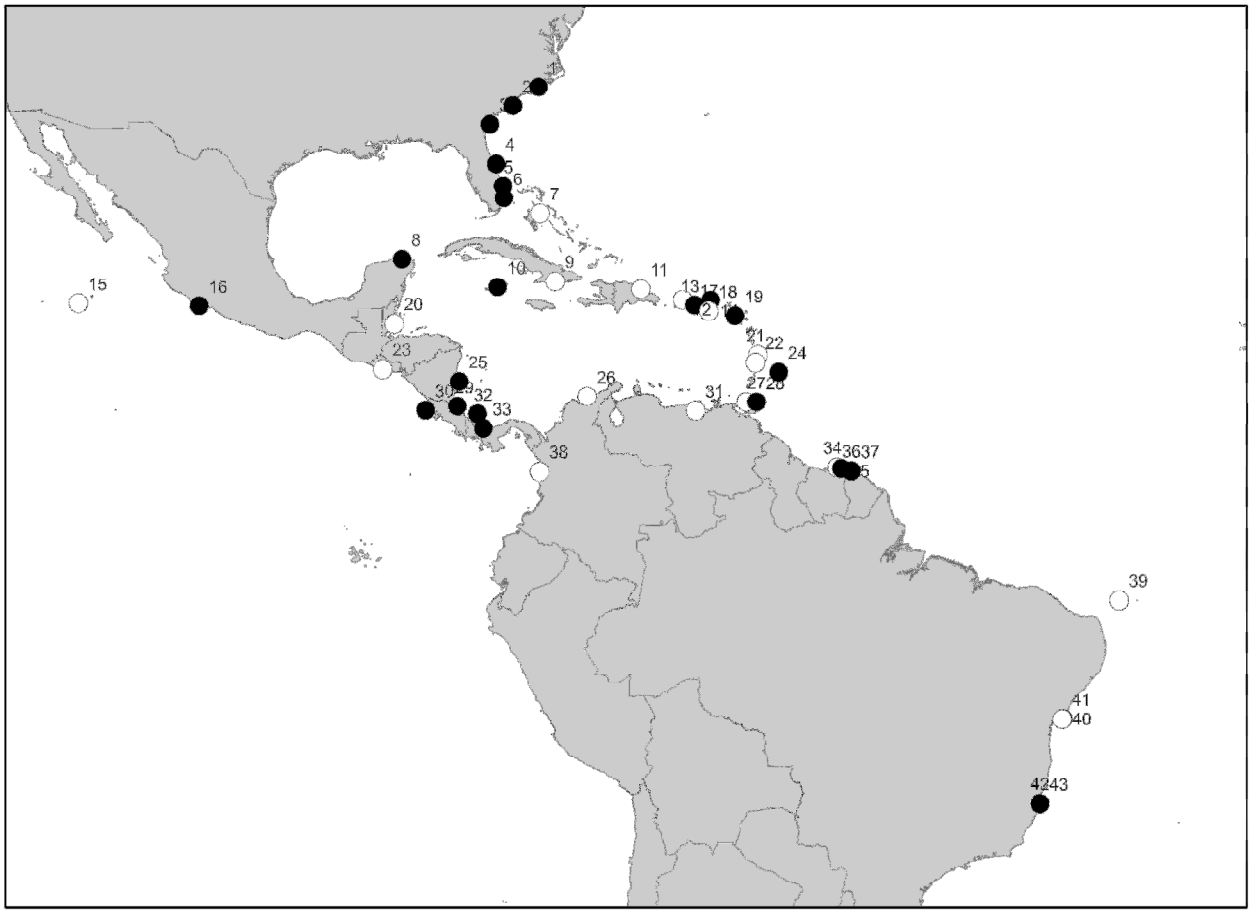
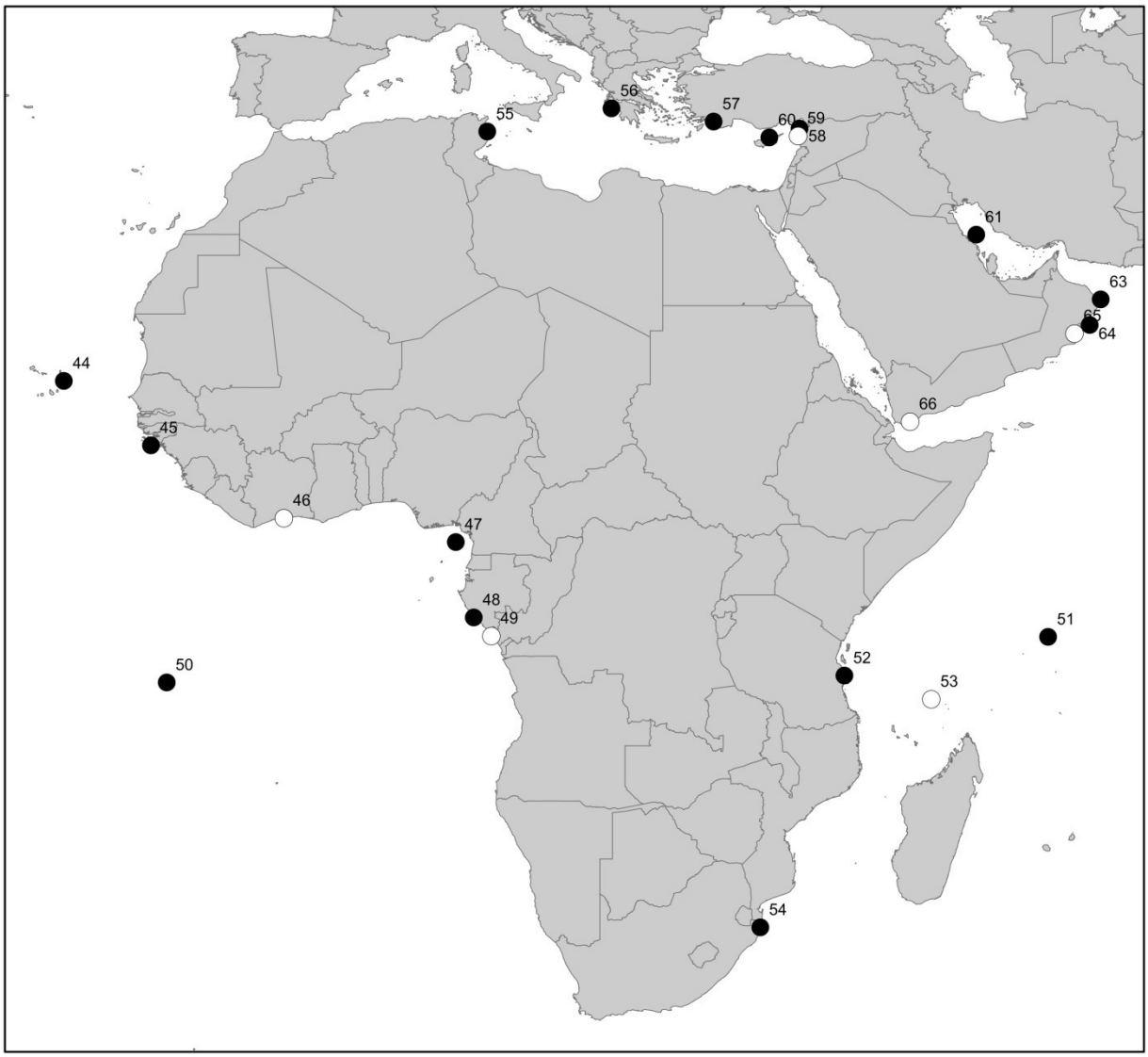


Fig. 1



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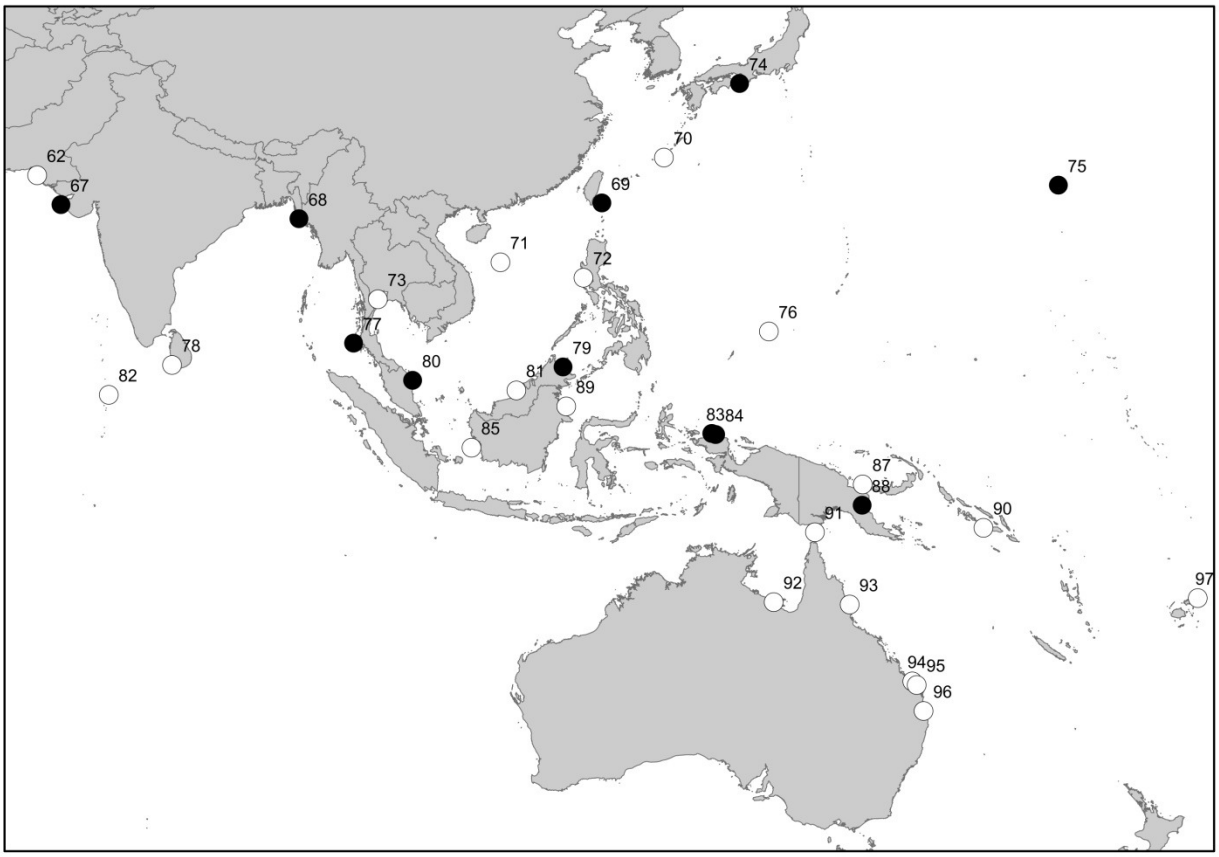
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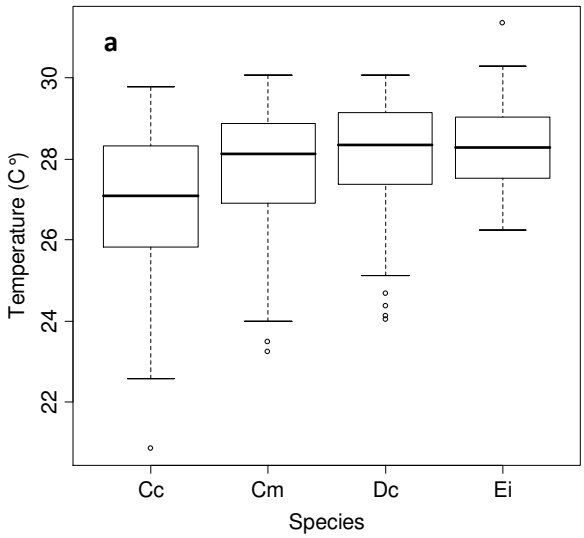
Fig. 3


a
Temperature (C°)
22
24
26
28
30
Cc
Cm
Dc
Ei
Species

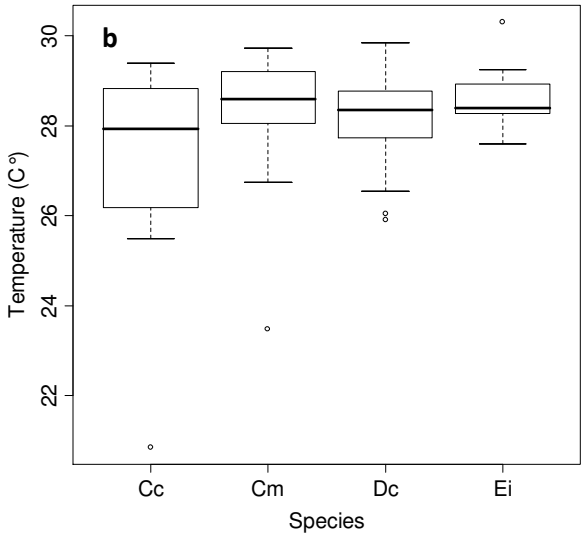
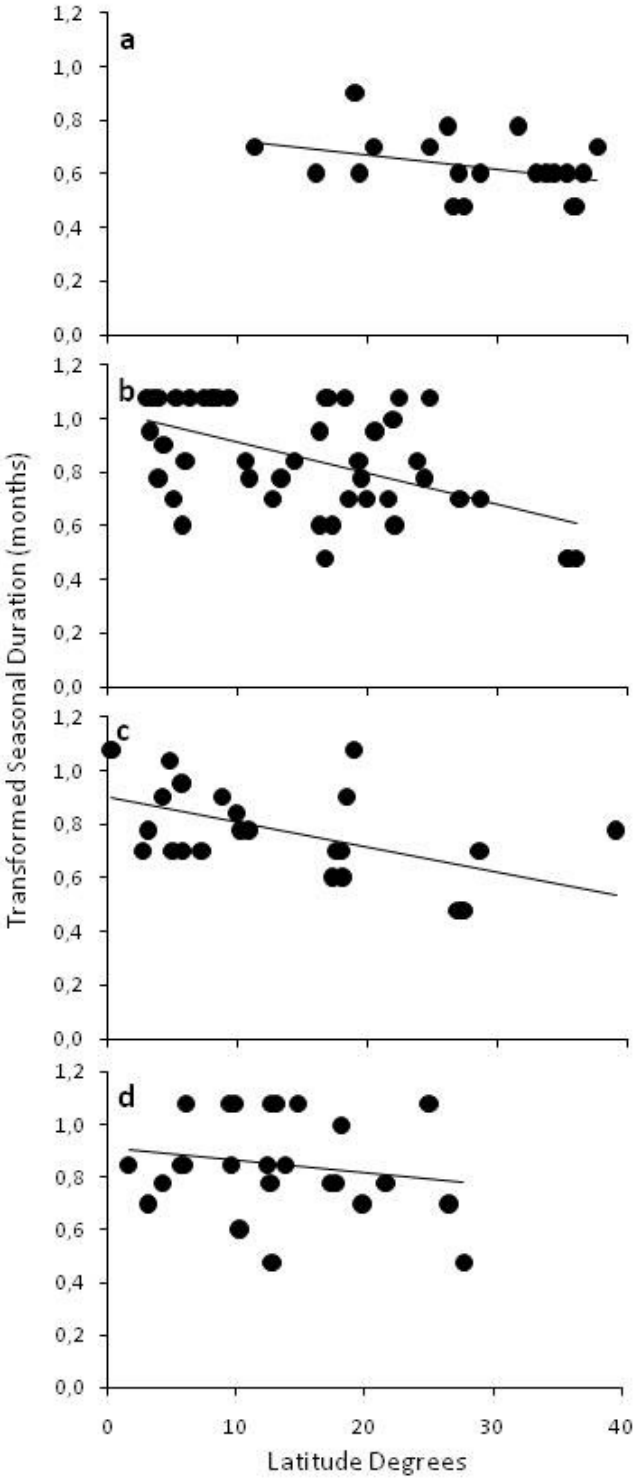

b
Temperature (C°)
22
24
26
28
30
Cc
Cm
Dc
Ei
Species

Fig.4


a
b
c
d
Transformed Seasonal Duration (months)
Latitude Degrees
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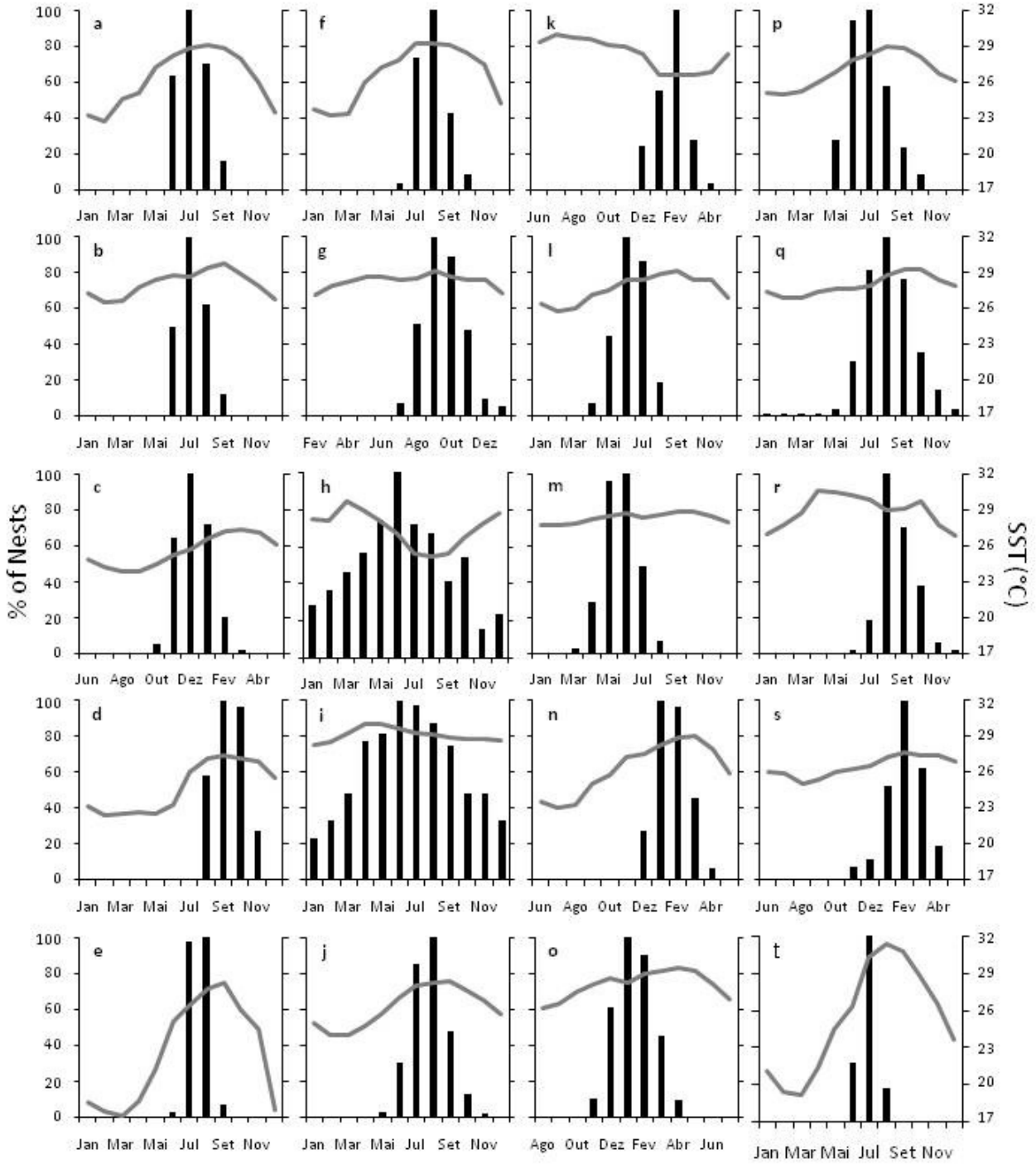
0,6
0,8
1,0
1,2
0
10
20
30
40

Fig.5


% of Nests
SST (°C)
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q
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Jan Mar Mai Jul Set Nov
Fev Abr Jun Ago Out Dez
Jun Ago Out Dez Fev Abr
Ago Out Dez Fev Abr Jun

Fig. 6